GERMINATION AND ESTABLISHMENT OF *PINUS CONTORTA* VAR. *MURRAYANA* (PINACEAE) IN MOUNTAIN MEADOWS OF YOSEMITE NATIONAL PARK, CALIFORNIA

JOHN A. HELMS
Department of Forestry and Resource Management,
University of California, Berkeley 94720

RAYMOND D. RATLIFF
USDA Forest Service, Pacific Southwest Forest and
Range Experiment Station,
2081 E. Sierra Ave., Fresno, California 93710

ABSTRACT

Pinus contorta var. *murrayana* (lodgepole pine) commonly invades mountain meadows. Studies were made on a wet and a dry meadow in Yosemite National Park, California, to determine differences in meadow habitat as defined by differences in composition and cover of herbaceous vegetation, soil characteristics, and physiography. Site ordination identified species on sites of decreasing moisture content. In both fall and spring, *P. contorta* seeds were sown on both covered and uncovered plots in each of 12 meadow sites. Germination and survival of seeds were measured for three consecutive years. Invasion of pine was uncommon on both the wetter meadow, dominated by *Aster alpigenus, Carex nebraskensis,* and *Deschampsia caespitosa,* and on the driest sites characterized by *Lupinus confertus* and *Horkelia fusca* subsp. *capitata.* Most invasion occurred on moderately dry sites dominated by *Aster occidentalis, Trifolium longipes,* and *Danthonia californica.* Differences in germination from fall and spring seeding were not significant. Depredation by rodents and birds reduced germination and survival on the uncovered seed plots by approximately 50%.

Pinus contorta Dougl. ex Loud. var. *murrayana* (Grev. & Balf.) Engelm. (lodgepole pine) commonly invades mountain meadows in the Sierra Nevada of California. Invasion is sporadic and the factors that limit germination and establishment of pine seedlings in meadows are not well understood. The invasion is important in meadow succession and is of concern to resource managers who are responsible for meadow conservation and management.

Mountain meadows differ substantially in topography, water availability, and microclimate. These differences occur as within- and between-meadow variation in timing of snow melt, drainage patterns, and vegetative cover. These factors probably also influence the timing and extent of lodgepole pine seedling establishment in meadows.

Germination of lodgepole pine is abundant in full sunlight, on bare mineral soil or disturbed duff, in the absence of competing

MADROÑO, Vol. 34, No. 2, pp. 77–90, 1987

vegetation, and with adequate soil moisture (Lotan 1964, Shepperd and Noble 1976, Lotan and Critchfield in press). Seedling mortality is associated commonly with high soil surface temperature, drought, soils with low water-holding capacity, unincorporated organic matter, and grazing (Cochran 1969, Lotan and Perry 1977, Lotan and Critchfield in press). Specific sites within meadows that are more favorable for pine establishment are indicated by the presence of 'outlier' trees. These trees are associated commonly with exposed rocks, logs, and groups of shrubs (Leonard et al. 1968, 1969) that are thought to provide higher soil temperature, more favorable soil texture and drainage, earlier snow melt, and protection from browsing.

This study was designed to contribute to the knowledge of lodgepole pine germination and to examine more closely within- and between-meadow variability in establishment of pine seedlings. Specific objectives were to determine the extent to which successful establishment is associated with: 1) availability of seeds and possible losses over the winter, 2) vegetative cover and soil water content, and 3) depredation by rodents and birds.

Study Area

Two meadows that had not been grazed recently by range cattle, one large and wet and the other small and dry, were studied in California's Yosemite National Park. These meadows are located at 2100 m near Glacier Point Road on the trail to Lost Bear Meadow (Fig. 1). Both meadows are surrounded by lodgepole pine stands, have vegetated rather than sandy margins, and are montane rather than subalpine. The larger site (3.37 ha) has topography of type A, formed in a basin; the smaller site (1.83 ha) is type C, formed along a permanent stream (Ratliff 1985). The larger meadow ranges from good to excellent condition, i.e., having no abnormal erosion and with herbage production near the climatic potential. The smaller meadow ranges from good to very poor condition. The poorest conditions occur near the stream channel, which is a continuous gully 1–2 m deep where erosion has lowered the water table.

Several study sites (areas that differ in species composition; Ratliff 1982) occur in each meadow. They represent different meadow series as defined by their hydrologic and vegetative classifications (Ratliff 1985).

Methods

Study sites. In late summer of 1981, five sites (sites 1–5) on the large meadow and four (sites 6–9) on the small meadow were selected to represent different microenvironments that could influence the

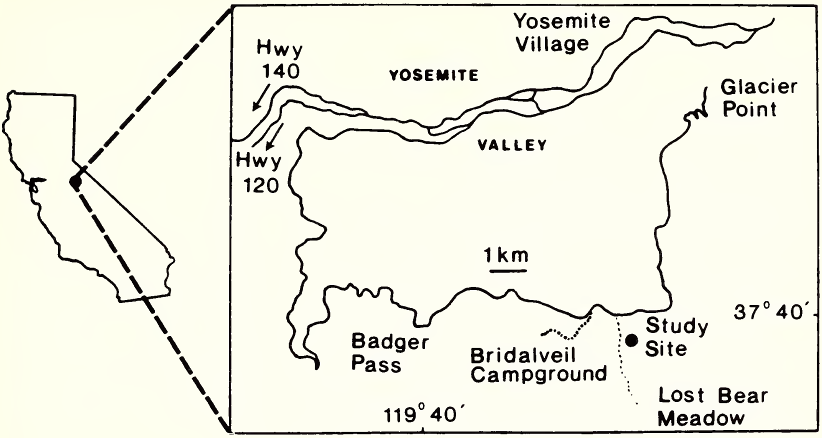


FIG. 1. Location of study.

success of lodgepole pine seedling establishment. Size and shape of sites varied with vegetation boundaries, but contained no less than 100 m^2. Because of small floristic differences, sites 2, 6, and 9 were subdivided for vegetation analysis. Rather than measure topography and microclimate directly, we evaluated site differences using floristic characteristics. This approach presumes that frequency and cover of particular herbaceous species are related to differences among microenvironments within the meadows, and that different species and their relative cover influence the capacity of lodgepole pine to invade meadows.

On each site, species frequencies were estimated using 100 randomly located 10 × 10 cm quadrats. Foliar cover (proportion of area under live aerial parts) and species composition were estimated at each seed plot. Site and species ordinations were derived from these data by reciprocal averaging (Hill 1973).

Soil characteristics near the center of each site were compared by taking a soil sample from the 10–20 cm depth. Samples were analyzed for: 1) percent sand, silt, and clay (estimated by the hydrometer method; Bouyoucos 1936); 2) percent organic matter [estimated by the loss on ignition method (ignition was for 4 hr at 600°C), Nelson and Sommers 1982]; 3) pH (estimated by the soil-water paste method with ionanalyzer; McLean 1982); and 4) bulk density at 0–10 cm and 10–20 cm depths [estimated by the cylinder (known volume) method, Cook and Stubbendieck 1986].

Soil depth to consolidated material was estimated using a probe, and depth to the water table was determined prior to fall precipitation in October 1983.

Seed plots. Ten replications of both uncovered and covered 0.1

m^2 plots containing approximately 50 seeds were established on each of the 12 sites in the fall of 1981 and again in the spring of 1982. Seeds were obtained from cones collected in 1981 from trees in an adjacent area. Seeds sown in the fall were unstratified. Spring sowing after snow melt utilized stratified seeds (soaked one day, held at 1.5°C in plastic bags for 28 days, sown wet; USDA 1974) to simulate the treatment that seeds receive as they overwinter on the meadows. Covers were made from 1.3-cm-mesh wire screen.

The number of seedlings in each plot was counted four times during the growing season in 1982, and also at the end of summer in both 1983 and 1984. Tests for significance of differences between mean survival at the end of three growing seasons were made using the Kruskal-Wallis non-parametric test for differences in means of ranked data grouped by single classification (Conover 1980). All plant nomenclature follows Munz (1959).

RESULTS

Vegetation

Twenty-three herbaceous species were found on both meadows; an additional 27 species occurred only on the large meadow and an additional 20 occurred only on the small meadow. Species with frequencies of 20% or more on at least two sites were used for vegetation analyses. The single axis reciprocal averaging ordinations of species frequency and composition data described similar arrays of herbaceous species on sites of decreasing moisture content. Consequently, species composition of the seed plots adequately defined the microenvironments of each site (Table 1).

Species most representative of wetter conditions (sites 4, 3, 5) were *Aster alpigenus, Carex nebraskensis, C. rostrata, Deschampsia caespitosa, Juncus orthophyllus,* and *Phalacroseris bolanderi* (Table 1). The moderately dry sites (sites 2, 6, 7, 1) were characterized by abundant *Aster occidentalis, Danthonia californica,* and *Trifolium longipes.* Species most representative of dry conditions (sites 8, 9) were *Horkelia fusca* subsp. *capitata, Lupinus confertus,* and *Penstemon rydbergii.*

Soils

Ordination of the sites from wettest to driest generally reflected increasing depths to the water table (Table 2). This shows a close relationship between species frequency, composition, and soil water availability. Also, with the gradient from wet to dry sites, organic matter decreased, and both bulk density (0–10 cm depth) and acidity increased. Soil textures and depths showed no apparent relationship to the moisture gradient.

TABLE 1. AVERAGE FOLIAR COVER AND SPECIES COMPOSITION OF SEED PLOTS AT 12 MEADOW SITES. Site ordination approximates a decreasing soil moisture gradient (left to right).

	Site											
	Wetter										Drier	
Characteristics	4	3	5	2b	2a	6b	6a	7	1	8	9a	9b
Foliar cover (%)	82.5	89.0	74.5	87.0	74.0	82.9	76.2	28.3	85.8	30.0	86.9	67.5
Composition (% foliar cover)												
Phalacroseris bolanderi	43.5	14.0	1.0									
Carex rostrata		5.0	6.0				0.6					
Deschampsia caespitosa		0.5	24.0	6.0								
Carex nebraskensis	3.5	11.0		6.5	5.5							
Aster alpigenus	11.0	9.0	7.5	1.0	3.5				3.0			
Juncus orthophyllus	0.5	0.5	0.5						0.2			
Eleocharis pauciflora	32.0	41.5	4.5	34.0	24.0	25.0	35.6					
Hypericum anagalloides			1.0	4.5	1.0	0.4						
Mimulus primuloides	0.5		8.5	1.0						2.0		
Juncus balticus		0.5	0.5	5.0	0.5		1.9		0.5			
Perideridia bolanderi	3.5	4.0	5.5	2.5	6.5	3.3	7.5	1.9	0.8	0.5		
Trifolium longipes			0.5	0.5	11.5	18.8			5.2			
Danthonia californica			2.5	4.5	9.5	17.5	16.9	5.8	6.0	2.0		
Muhlenbergia filiformis	3.5	10.0	5.5	18.0	16.0	1.7		3.9	12.8	33.5		
Aster occidentalis			0.5	4.0	14.0	29.6	31.9	77.2	27.5	23.0	1.9	
Stipa columbiana								2.2	8.8	0.5		
Agrostis idahoensis								1.9		5.5		
Penstemon rydbergii							3.1	6.9	3.0	14.8	10.0	7.0
Lupinus confertus										4.2	10.0	6.0
Horkelia fusca subsp. *capitata*									3.5		74.4	87.0

Table 2. Soil Physical Characteristics of 12 Meadow Sites. Site ordination approximates a decreasing soil moisture gradient (left to right). SL = Sandy Loam; LS = Loamy Sand.

	Site											
	Wetter										Drier	
Characteristic	4	3	5	2b	2a	6b	6a	7	1	8	9a	9b
Soil texture												
% sand	54.3	69.0	71.3	73.9	80.5	65.4	67.3	69.3	80.6	59.8	63.4	67.4
% silt	41.8	27.2	26.8	22.4	17.6	30.0	29.0	27.0	15.7	36.5	30.9	28.8
% clay	3.9	3.8	1.9	3.7	1.9	4.7	3.7	3.7	3.7	3.7	5.6	3.7
Class	SL	SL	SL	LS	LS	SL	SL	SL	LS	SL	SL	SL
Organic matter (%)	34.3	14.3	22.2	11.1	8.5	11.5	10.7	8.7	6.9	11.1	12.4	8.5
Acidity (pH)	4.8	4.7	4.8	4.8	5.0	4.9	4.9	4.5	4.7	4.9	4.3	4.5
Bulk density (g-cm^3)												
0–10 cm depth	0.22	0.29	0.37	0.52	0.74	0.77	0.72	0.91	1.01	0.85	0.82	0.93
10–20 cm depth	0.37	0.62	0.47	0.89	0.86	0.81	0.78	1.04	1.14	0.85	0.80	0.92
Soil depth (cm)	75	200	142	193	116	75	126	140	109	71	146	182
Water depth on 7 October 1983 (cm)	2	6	12	7	20	50	47	58	40	78	84	72

TABLE 3. THE NUMBER OF SURVIVING LODGEPOLE PINE SEEDLINGS PER SEED PLOT AT THE END OF THE THIRD GROWING SEASON AFTER SOWING 50 SOUND SEED PER PLOT. Site ordination corresponds to a decreasing soil moisture gradient (left to right) shown in Table 1.

		Site								
	4	3	5	2	6	7	1	8	9	Mean
Fall-sown: covered	0	0	0.4	5.6	3.1	29.5	0.0	10.7	0.1	5.48
uncovered	0	0	0	0.1	0.8	7.3	0.0	3.5	0	1.30
Spring-sown: covered	0	0	0	3.8	1.4	19.6	7.8	8.7	0.3	4.62
uncovered	0	0	0	0.7	1.7	11.2	2.1	3.5	0	2.13

Seed Plots

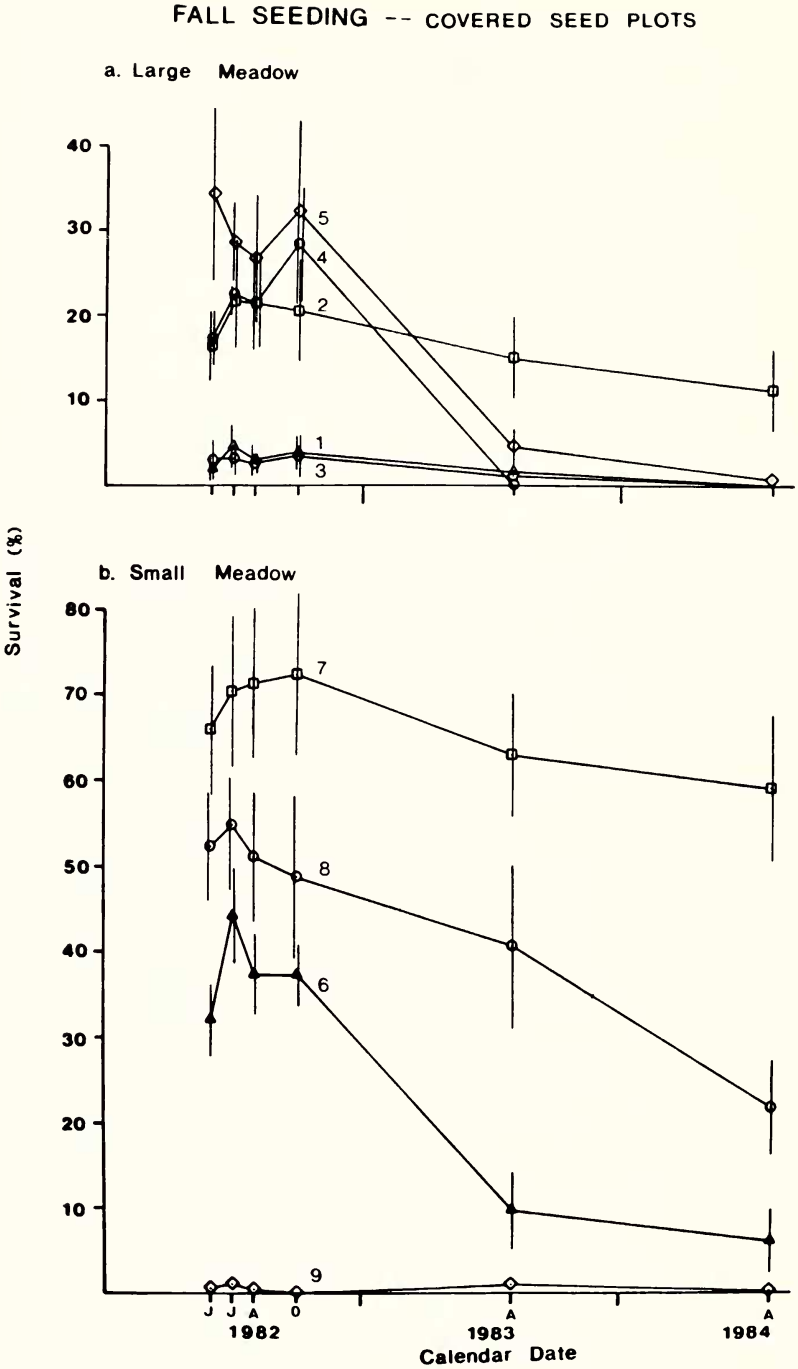
Fall seeding: covered seeds. On the large meadow, survival during the first year after sowing on sites 2, 4, and 5 was 20–30% and was substantially greater than the 2–4% survival on sites 1 and 3 (Fig. 2a). In the second year, survival on all sites except site 2 decreased rapidly. By year 3, survival on sites 1, 3, and 4 was zero (Table 3). On site 5, survival of 0.8% was lower ($p = 0.10$) than the 11.2% on site 2.

On the small meadow, seedling survival at the end of the first year was generally much higher (72.4, 48.8, 37.4, and 0%, respectively on sites 7, 8, 6, and 9). In subsequent years, survival decreased until by year three it was 59.0, 21.4, 6.2, and 0.2%, respectively. Mean survival on site 7 was significantly greater ($p = 0.05$) than on sites 8 and 6, and survival on site 8 was greater ($p = 0.10$) than on site 6.

Fall seeding: uncovered seeds. On the large meadow at the end of the first year, survival was 28.0, 15.6, 4.0, 3.6, and 0%, respectively on sites 4, 5, 3, 2, and 1 (Fig. 3a). By the end of year two, survival on all sites had become close to zero.

On the small meadow, survival at the end of the first year was 28.0, 18.6, 7.8, and 0%, respectively on sites 6, 7, 8, and 9 (Fig. 3b). Mean survival on site 7 was greater ($p = 0.10$) than that on site 8; however, the means of survival on sites 6 and 7 were not different at that same level of significance. By the end of year three, survival was 14.6, 7.0, 1.6, and 0%, respectively on sites 7, 8, 6, and 9. This ranking of sites was the same as that on the covered seed plots.

Spring seeding: covered seeds. On the large meadow, only sites 1 and 2 were sown because sites 3, 4, and 5 were under water until late summer. First-year survival on these two sites was 6.8 and 11.8%, respectively (Fig. 4). Second-year survival on site 1 increased to 28.1%, indicating additional germination of seeds on this driest site in the second year after sowing. At the end of year three, the


FALL SEEDING -- COVERED SEED PLOTS
a. Large Meadow
40
30
20
10
5
4
2
1
3
Survival (%)
b. Small Meadow
80
70
60
50
40
30
20
10
7
8
6
9
J
J
A
O
A
A
1982
1983
1984
Calendar Date

mean survival on plots 1 and 2 was 15.6 and 7.6%, respectively, and these means were not different (p = 0.10).

On the small meadow, survival at the end of the first year was 47.4, 45.2, 25.4, and 0% on sites 8, 6, 7, and 9, respectively (Fig. 4b). Additional germination of seeds in the second year occurred on the driest sites 7 and 9. By the end of year three, survival was 38.2, 17.8, 2.8, and 0.7%, respectively in sites 7, 8, 6, and 9. Using p = 0.10 as a test of significance, the means of survival on sites 6 and 8, and on sites 7 and 8, were different, but means of survival on sites 6 and 9 were not.

Spring seeding: uncovered seeds. On the large meadow, the extent and pattern of survival were similar to those in the covered spots (Fig. 5a), but survival at the end of the third year was only 4.2% on site 1 and 1.4% on site 2, respectively; the difference between these means was not significant (p = 0.10).

On the small meadow, survival at the end of the first year on sites 6, 8, 7, and 9 was 18.0, 16.4, 14.0, and 0%, respectively (Fig. 5b). Sites 7 and 9 showed additional germination during the second year after sowing. By the end of year three, survival was 22.4, 7.0, 3.4, and 0% for plots 7, 8, 6, and 9, respectively. The difference between mean survival on sites 7 and 8 was significant (p = 0.05), whereas that between sites 6 and 8 was not.

DISCUSSION

Seed availability. Direct seeding of lodgepole pine showed that pine establishment in meadows is associated less with seed availability than with meadow type. On the wetter meadow, applying seeds in the fall to simulate natural seed fall showed that, despite abundant seeds, no seedlings survived through the second year (Fig. 3). On the drier meadow, up to 14% survival by the end of the third year indicates that invasion of this meadow type is much more likely (Fig. 3). Generally, for each meadow site, differences in survival between seeding in the fall and spring (Figs. 2 and 4; Figs. 3 and 5) were non-significant. This suggests that overwinter decreases in germinability and physical movement of seed off the site by melting snow are not important factors in the establishment of lodgepole pine.

Depredation. The similarity of pine seedling survival in covered

---

←

FIG. 2. Survival of lodgepole pine seedlings on fall-seeded, covered plots on sites 1–9 for the large and small meadows. Bars indicate standard errors of means; letters indicate months.

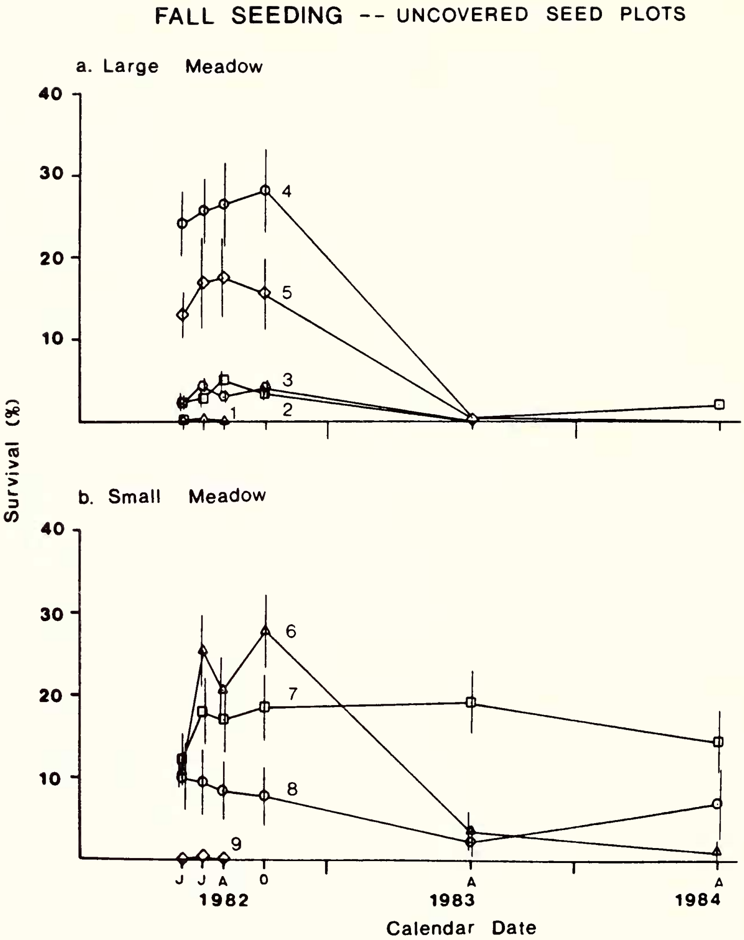


FIG. 3. Survival of lodgepole pine seedlings on fall-seeded, uncovered plots on sites 1–9 on the large and small meadows. Bars indicate standard errors of means; letters indicate months.

and uncovered fall-seeded plots on the large meadow (except for the drier site 2) (Figs. 2 and 3) suggests that depredation by rodents and birds on wet sites is unimportant. Covered, spring-seeded plots on the large meadow, however, had approximately twice the survival of the corresponding uncovered plots at each measurement date (Figs. 4 and 5).

Depredation was most apparent on the drier small meadow where germination and survival on uncovered fall-seeded plots were reduced by approximately 50% (Figs. 2 and 3). The effect of covering seeds and seedlings was less apparent on spring-seeded plots, with

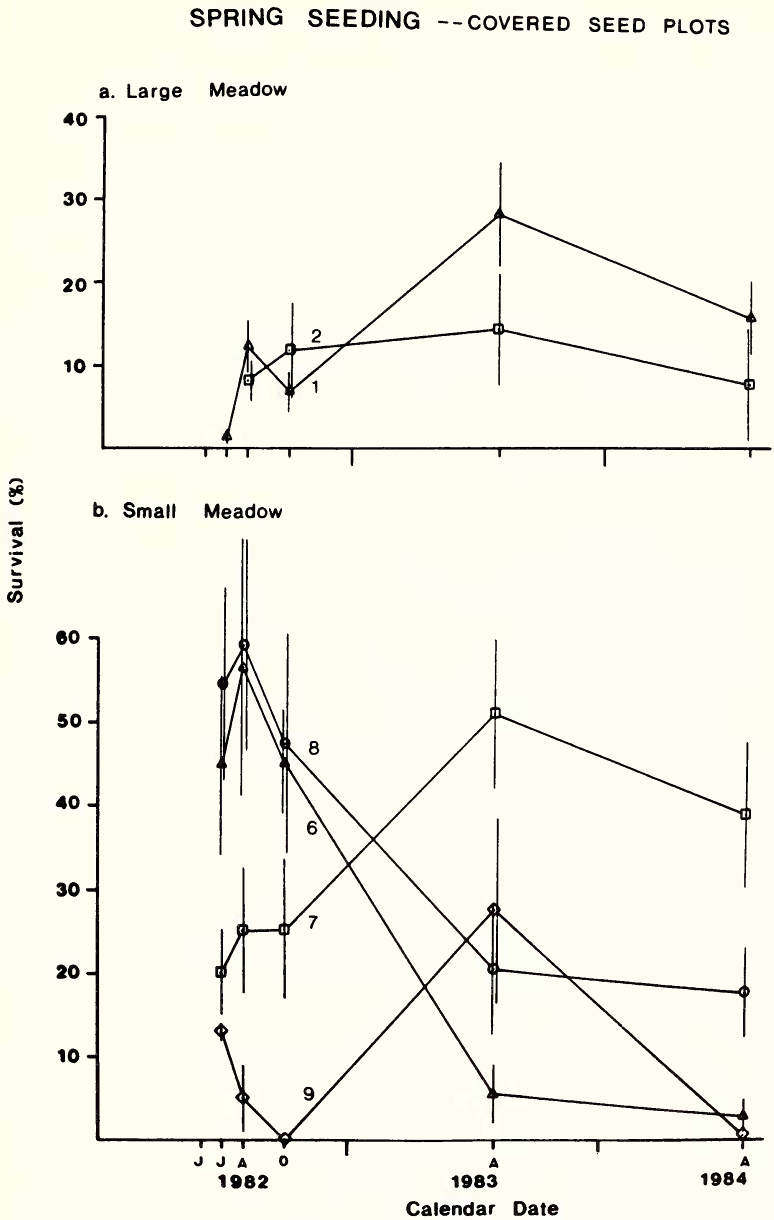


FIG. 4. Survival of lodgepole pine seedlings on spring-seeded, covered plots on sites 1–9 on the large and small meadows. Bars indicate standard errors of means; letters indicate months.

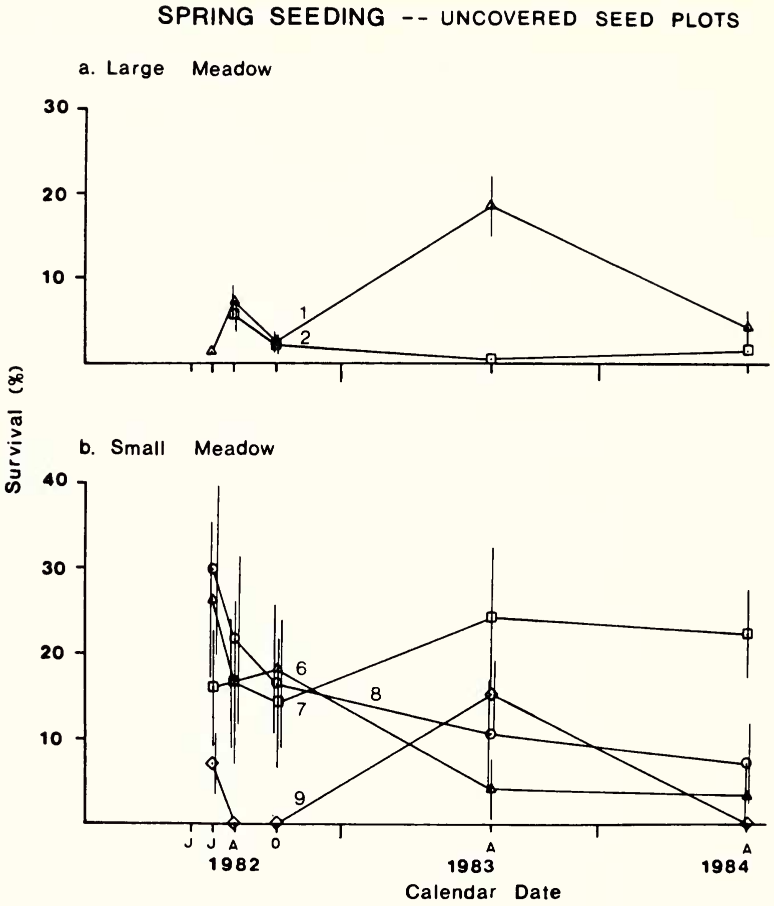


FIG. 5. Survival of lodgepole pine seedlings on spring-seeded, uncovered plots on sites 1–9 on the large and small meadows. Bars indicate standard errors of means; letters indicate months.

the notable exceptions of site 7 where seeds were sown on soil bare from gopher activity, and of site 8 that had only 30% foliar cover (Figs. 4 and 5). The greater survival of seedlings on the small meadow corresponds with its having a much larger number of previously-established outlier lodgepole pine trees.

Increased number of seedlings in the second year on the drier spring-seeded plots, 1, 7, and 9, may be associated with possible delayed germination of some seeds. This increase of approximately 8–25 seedlings per 0.1 m^2 plot probably is too large to be explained entirely by additional naturally-dispersed seeds. No new seedlings were observed adjacent to the plots.

Meadow type. Differences in frequency and cover of herbaceous species across meadows reflect differences in moisture regimes and potential for pine invasion. High potential occurs on moderately dry sites. These sites are usually too wet early in the year for much seed and seedling depredation. Later, these sites are not saturated but remain moist, which improves chances for establishment. Low potential occurs in the wettest and driest sites where either continuous saturation or moisture stress tends to prevent establishment.

ACKNOWLEDGMENTS

This study was supported by the USDA Forest Service, Pacific Southwest Forest and Range Experiment Station, Berkeley, California, Project Number PSW-80-0022. It also was part of the University of California's Agricultural Experiment Station Project 2942-MS. We thank Drs. W. Critchfield and F. Vasek for their constructive reviews and suggestions for improving the manuscript.

LITERATURE CITED

BOUYOUCOS, C. J. 1936. Directions for making mechanical analysis of soils by the hydrometer method. Soil Science 42:225–228.

COCHRAN, P. H. 1969. Thermal properties and surface temperatures of seedbed: a guide for foresters. U.S.D.A. Forest Serv. Pacific Northw. Forest and Range Exp. Sta., Portland, OR.

CONOVER, W. J. 1980. Practical nonparametric statistics. John Wiley and Sons, New York.

COOK, C. W. and J. STUBBENDIECK, eds. 1986. Range research: basic problems and techniques. Soc. for Range Management, Denver, CO.

HILL, M. O. 1973. Reciprocal averaging: an eigenvector method of ordination. J. Ecology 61:237–249.

LEONARD, R., D. HARKIN, and P. J. ZINKE. 1968. Ecological study of meadows in lower Rock Creek, Sequoia National Park: progress report for 1967. Copy on file at U.S.D.A. Forest Serv. Pacific Northw. Forest and Range Exp. Sta., Fresno, CA.

———, C. M. JOHNSON, and P. J. ZINKE. 1969. Ecological study of meadows in lower Rock Creek, Sequoia National Park: progress report for 1968. Copy on file at U.S.D.A. Forest Serv. Pacific Northw. Forest and Range Exp. Sta., Fresno, CA.

LOTAN, J. E. 1964. Initial germination and survival of lodgepole pine on prepared seedbeds. U.S.D.A. Forest Serv. Res. Note INT–29.

——— and W. B. CRITCHFIELD. In press. *Pinus contorta. In* Silvics of forest trees of North America. U.S.D.A. Forest Serv. Pacific Southw. Forest and Range Exp. Sta., Berkeley, CA.

——— and D. A. PERRY. 1977. Fifth-year seed: seedling ratios of lodgepole pine by habitat type and seedbed preparation technique. U.S.D.A. Forest Serv. Res. Note INT–148.

MCLEAN, E. O. 1982. Soil pH and lime requirement. *In* A. L. Page, R. H. Miller, and D. R. Keeney, eds., Methods of soil analysis, Part 2. Chemical and microbiological properties—agronomy monograph 9 (2nd ed.), p. 199–224. ASA-SSSA, Madison, WI.

MUNZ, P. A. 1959. A California flora. Univ. California Press, Berkeley.

NELSON, D. W. and L. E. SOMMERS. 1982. Total carbon, organic carbon and organic matter. *In* A. L. Page, R. H. Miller, and D. R. Keeney, eds., Methods of soil analysis, Part 2. Chemical and microbiological properties—agronomy monograph 9 (2nd ed.), p. 539–579. ASA-SSSA, Madison, WI.

Ratliff, R. D. 1982. A meadow site classification for the Sierra Nevada, California. U.S.D.A. Forest Serv. Pacific Southw. Forest and Range Exp. Sta. Gen. Tech. Rep. PSW-60.

———. 1985. Meadows in the Sierra Nevada of California: state of knowledge. U.S.D.A. Forest Serv. Pacific Southw. Forest and Range Exp. Sta. Gen. Tech. Rep. PSW-84.

Shepperd, W. D. and D. L. Noble. 1976. Germination, survival, and growth of lodgepole pine under simulated precipitation regimes: a greenhouse study. U.S.D.A. Forest Serv. Res. Note RM-328.

USDA. 1974. Seeds of woody plants in the United States. Agric. Hdb. No. 450. U.S.D.A. Forest Serv., Washington, DC.

(Received 6 Sep 1985; revision accepted 15 Dec 1986.)

ANNOUNCEMENT

Women Botanists Recount Career Hardships and Highlights

Three women botanists describe the highlights of their careers as herbarium curators, collectors of native and ornamental plants, and conservationists of flora and habitat in this initial volume of a new series of oral histories on California Women in Botany. Produced by the University of California's Regional Oral History Office, the volume challenges the traditional view of botany as the pastime for the "weaker sex."

The vivid tales of UC Herbarium botanist Annetta Carter, describing collecting trips to Baja California with the eighty-year-old Annie Alexander, attest to the hardships and joys of life in the field. Owens Valley botanist Mary DeDecker's recounting of her battles to protect the fragile habitat of her beloved desert plants reflects great strength of purpose and fearless, informed persistence. Elizabeth McClintock's dedicated work for the California Academy of Sciences herbarium reveals a third aspect of the many contributions of California women botanists.

California Women in Botany is available for study at The Bancroft Library, UC Berkeley, and at the UCLA Library Department of Special Collections. The volume may be purchased from Friends of the Bancroft Library, Regional Oral History Office, Univ. of California, Berkeley 94720. Price: $45.00.